V. "Contributions to the Life-History of the Foraminifera." By J. J. Lister, M.A., St. John's College, Cambridge. Communicated by Professor Alfred Newton, F.R.S. Received May 7, 1894.

(Abstract.)

The phenomenon of dimorphism is now known to be presented by many different species of Foraminifera.

The individuals of a species fall into two groups. In one the central chamber (the *Megasphere* of Munier-Chalmas and Schlumberger) is of considerable size, while in the other it is small (*Microsphere*). These two forms of a species may be distinguished as the *Megalospheric* and *Microspheric* forms.

They have been shown to differ, not only in the size of the central chamber, but, in some instances (Miliolidæ), in the plan on which the chambers are arranged, in the size attained by the full-grown shell, and also in the frequency of their occurrence, the megalospheric form being much the more abundant.

It has been suggested that the different conditions under which *Orbulina universa* is found represent the megalospheric and microspheric forms, but the reasons urged in favour of this view appear inconclusive.

Polystomella crispa (*Linn.*).

With the hope of throwing light on the life history of the Foraminifera, a large number of specimens of this species have been examined.

Like so many others, it is dimorphic. Though the two forms are indistinguishable when the shell is complete, on examining decalcified and stained specimens they may be at once referred to one form or the other. The central chamber of the megalospheric form is generally about 80 μ in diameter, while that of the microspheric form is about 10 μ. Associated with the difference in the size of the central chambers there is a marked difference in the nuclei of the two forms. The relative frequency of the megalospheric form to the microspheric in 1812 examples, is as 34 to 1.

In the *Microspheric* form numbers of small nuclei are present, scattered through the protoplasm, but not extending into the terminal chambers. Those in the inner chamber are smaller than those situated further on. The nuclei contain nucleoli of different sizes lying in an apparently homogeneous internucleolar substance. It is shown that the nuclei increase in number by simple division, and it appears probable that they are so derived from a single nucleus.

After maintaining their rounded form for a certain time, the nuclei give off portions of their substance into the surrounding protoplasm. This process appears to begin in the innermost chambers, but it extends to the nuclei in the outermost chambers, and ultimately the whole of the nuclear material is distributed through the protoplasm in the form, in preserved specimens, of irregularly branched and deeply staining strands. Of the further history of the microspheric form I have no clear evidence.

The *Megalospheric* form during the vegetative period of its life has a single large nucleus, which grows in size with the growth of the protoplasm, and passes on from chamber to chamber, moving towards the centre of the protoplasm contained in the series of chambers, though lagging some distance short of it. It consists of a nuclear reticulum, nucleoli which occupy the nodes of the reticulum, and of a substance occupying the meshes. The nucleoli appear to increase in number and diminish in size with the advance of the organism. There is reason to believe that as the nucleus moves on through the chambers portions of its substance are given off into the protoplasm. It appears that this may occur either by the separation of considerable portions, sometimes containing several nucleoli, which lie strewn along the track of the nucleus, or by the dispersal of minute fragments into the surrounding protoplasm, causing in stained specimens a flush in the neighbourhood of the nucleus. In some specimens the nucleus has lost its rounded form, and sends irregular processes into the protoplasm. Its staining properties are at the same time diminished. It appears probable that these nuclei are such as have given off a large part of their substances as above described, and are now in process of dissolution.

In the reproductive phase no large nucleus is present, but hosts of minute nuclei (1—2μ in diameter) are found scattered through the protoplasm. At the same time broad channels of communication have become opened up, setting the inner chambers in direct communication with the outer.

At first the small nuclei are most abundant in the terminal chambers, but ultimately they become uniformly distributed through the protoplasm. They then divide by karyokinesis, the protoplasm being aggregated about them in spherical masses, 3·5μ in diameter, each of which contains a dividing nucleus.

At a later stage each nucleus, presumably the daughter-nuclei of this division, becomes the centre of a flagellated spore. These spores are all of approximately equal size, in other words, they are *isospores*.

In one instance spores of a different character were observed escaping. These were *anisospores*. They consisted of *macrospores*, globular bodies having a diameter of 11—10μ, and with indications of a flagellum, and *microspores* of a globular or oval shape, from

6—1 μ in diameter and provided with two flagella, one longer than the other, rising close together from the body of the spore. I am unable to say whether the parent of these spores was megalospheric or microspheric, but as the isospores are produced by the individuals of the former type it is possible that the anisospores belong to those of the latter.

Orbitolites complanata, Lamk.

In the *Microspheric* form, the centre of the disc is occupied by small chambers. Numbers of rounded nuclei are distributed through the protoplasm, often in pairs, and in some cases they may be seen to be united by a constricted band, as though in process of simple division. Larger solitary nuclei with a well marked reticulum are also present.

In the later stages of growth large brood chambers are formed at the periphery of the disc, which Brady found to be crowded with young ("primitive discs") of the megalospheric form. Examination of specimens preserved in spirit in which the young are present in the brood chambers, shows that the inner part of the shell is empty, its contents being represented only by the young. A large nucleus is present in the "primordial chambers" of the young discs.

The centre of the *Megalospheric* form is occupied by the "primitive disc." This consists of a large "primordial chamber" (the megalosphere), which is usually pyriform, and measures about 100μ in length, surrounded by the very large "circumambient chamber." The small chambers of the remainder of the disc are arranged about the primitive disc in rings.

The nucleus which, as has been said, occupies the primordial chamber in the young form, maintains that position during a large part of the growth of the shell. Ultimately it appears to break up into irregular fragments, which become dispersed through the adjoining chambers.

The specimens of this form from Celebes have all attained a larger size than those from Tonga and Fiji. In three cases (out of 114) the protoplasm has left the central region of the disc, and is massed in brood chambers at the periphery in the form of megalospheric young, exactly resembling in shape and size those borne by the microspheric form. It is thus established that both the megalospheric and microspheric forms of *Orbitolites* under certain circumstances, produce young of the megalospheric type.

An examination of specimens of *Rotalia beccarii* (*Linn.*), *Truncatulina lobatula*, *Walker and Jacob*, *Calcarina hispida*, *Brady*, and *Cycloclypeus* has furnished evidence of the relation of nuclear characters to the two forms of a species analogous to that obtained in *Polystomella.*

Summary and Conclusions.

The following statements relating to the life-history of the Foraminifera appear to be justified :—

1. The species are in a great number of cases dimorphic. The dimorphism has been stated to exist in twenty-three genera, belonging to four out of the ten families into which Brady divided the group.

2. The two forms differ from one another—

   (*a*) In the size of the central chamber. Their difference in this respect is in many cases very marked but may be slight (*Truncatulina*).

   (*b*) In the shape and mode of growth of the chambers succeeding the megalosphere and microsphere.

   (*c*) In the character of their nuclei. In this paper it is shown that in several species the microspheric form has many comparatively small nuclei, while the megalospheric form has a single large nucleus.

3. The megalospheric form of a species is much more numerous than the microspheric.

4. The megalospheric form has been seen to arise in some cases (at least seven genera) as a young individual already invested by a shell, produced in the terminal or peripheral chambers of the parent. While in some cases (*Orbitolites*) the parent of such megalospheric young was microspheric, in others (*Peneroplis*, *Orbitolites*) it was megalospheric.

5. Foraminifera, in certain conditions, give rise to active swarm cells.

These have been previously recorded in *Gromia* and *Cymbalopora*. In *Polystomella* the protoplasm of a megalospheric form was found broken up into swarm cells of uniform size (*isospores*), and similar bodies in a flagellated condition have been seen escaping.

The production of *anisospores* has been recorded in *Miliola* (Schneider), and it occurs also in *Polystomella* as stated above.

The question has arisen: are the two forms of the Foraminifera distinct from their origin, or is one a modification of the other? The following reasons may be urged for rejecting the latter hypothesis :—

Among the Miliolidæ the plan of growth is often entirely different in the two forms. The hypothesis of modification would in this case require a remodelling of the whole shell.

If such modification were to occur, various stages in the replacement of the megalosphere by small chambers should be found. So far as I am aware such stages have not been found.

While the megalospheric form is not found in process of transition into the microspheric, it is found, either with the protoplasm broken up into swarm cells (*Polystomella*), or containing megalospheric young in the peripheral chambers, while the central chambers are empty (*Orbitolites*). In both cases the megalosphere remained unabsorbed at the centre of the shell.

The microspheric form is found in the young condition.

The nuclear characters of the two forms are, at any rate, in the species which I have examined, quite distinct.

It appears then that it may safely be concluded that the microspheric and megalospheric forms are distinct from their origin.

What then is their relationship?

When two forms of a species are met with in animals or plants they generally either represent different sexes, or they are members of a recurring cycle of generations.

The hypothesis that the two forms of the Foraminifera represent the two sexes appears to be disproved by the fact that in *Orbitolites complanata*, both megalospheric and microspheric forms are found with the young of the megalospheric form (primitive discs) in their brood chambers. Other genera furnish analogous, though less complete evidence. Hence it is impossible to regard either form as male.

We turn then to the other hypothesis that the two forms are members of a recurring cycle of generations. On this view it is necessary to suppose, from the evidence afforded by *Orbitolites complanata*, in which both microspheric and megalospheric forms have been found with the young of the megalospheric form in their brood chambers, that the megalospheric form may, at any rate in some genera, be repeated for one or more generations, before the microspheric form recurs. No evidence of such a repetition has, however, been furnished by the examination of *Polystomella*.

The view that the life-history of the Foraminifera comprises more than one generation is in harmony with the fact that the nuclear history of the two forms in Polystomella, so far as it has been observed, presents resemblances to that which Brandt has recently described in *Thalassicola* among the Radiolaria. In this group, as is well known, the individuals of a species fall into two sets, those producing isospores and those producing anisospores, which are regarded as an asexual generation alternating with a sexual.

The simultaneous division of nuclei by karyokinesis immediately before the formation of the reproductive elements which was observed in the megalospheric form of *Polystomella* is a phenomenon of very general occurrence. A similar division has been shown to occur

in several genera of the *Mycetozoa* immediately before the formation of the spores, and it appears probable that the phenomenon is akin to the division of the micro-nucleus which precedes conjugation in the *Infusoria*, and to the division of nuclei which occurs in the maturation of the reproductive elements in the higher forms of animals and plants.

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